

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3605, 22 pp., 7 figures April 9, 2007

A New Platynotan Lizard (Diapsida: Squamata) from the Late Cretaceous Gobi Desert (*Ömnögov*), Mongolia

MARK A. NORELL,¹ KE-QIN GAO,² AND JACK CONRAD³

ABSTRACT

Here we describe a new diminutive varanoid from the Late Cretaceous Djadoktha Formation of Ömnogov, Mongolia. The new taxon, *Ovoo gurval*, was found in the Nemegt Basin at the locality of Little Ukhaa, a locality adjacent to the rich fossil beds of Ukhaa Tolgod. The new varanoid is similar to *Aiolosaurus oriens*, another small varanoid from the Ukhaa Tolgod locality and several diagnostic characters of *Ovoo gurval* are shared with *Aiolosaurus oriens*. *Ovoo gurval* also has a pair of unusual neomorphic ossifications on the skull roof overlying the frontonasal contact. Positionally, these are unlike any neomorphic ossifications in other squamates, and certainly can be distinguished from osteoderms found in some varanoids.

INTRODUCTION

Localities in Djadoktha and Djadoktha-like rocks (see Loope et al., 1998; Dashzeveg et al., 2005; Dingus et al., in press) have produced an extensive lizard fauna. Notable among these localities is Ukhaa Tolgod, which has produced several thousand specimens of fossil lizards (Dashzeveg et al., 1995). The

Djadoktha specimens represent a remarkable diversity, and especially with respect to varanoid lizards, which are usually only rarely encountered in fossil deposits. Well-preserved varanoids are important because not only is there an impressive living diversity (Pianka, 1995; Norell, 2004), but they also may hold the clues necessary to pinpoint the origins of groups like mosasaurs, aigialosaurs, and

¹ Division of Paleontology, American Museum of Natural History (norell@amnh.org).

² Department of Geology, Peking University, Beijing 100871, People's Republic of China; Research Associate, Division of Paleontology, American Museum of Natural History (kqgao@pku.edu.cn).

³ Division of Paleontology, American Museum of Natural History (jconrad@amnh.org).

snakes. This paper describes a diminutive new varanoid lizard (IGM 3/767) from a Late Cretaceous deposit exposed in the Gobi Desert, Mongolia.

ABBREVIATIONS

Institutional

| | |
|--------|--|
| AMNH-R | American Museum of Natural History, Division of Vertebrate Zoology, Reptiles |
| IGM | Institute of Geology, Mongolian Academy of Sciences |
| FMNH | Field Museum of Natural History |
| IGM | Institute of Geology, Mongolian Academy of Sciences |

Anatomical

Uppercase L and R as prefixes signify left and right respectively.

| | |
|------|------------------------------------|
| ch | choana |
| dplf | dorsal posterior lacrimal foramen |
| ect | ectopterygoid |
| f | frontal |
| iof | infraorbital foramen |
| j | jugal articulation |
| l | lacrimal |
| m | maxilla |
| mb | mystery bone |
| n | nasal |
| na | naris |
| p | palatine |
| pat | palatine teeth |
| po | postorbitofrontal |
| pf | prefrontal |
| pmx | premaxilla |
| pt | pterygoid |
| ptt | pterygoid teeth |
| sptm | septomaxilla |
| t | tooth |
| v | vomer |
| vplf | ventral posterior lacrimal foramen |

GEOLOGICAL OCCURRENCE

IGM 3/767 was collected at the Little Ukhaa locality (Dingus et al., in press; Makovicky et al., 2003), Omnogov Aimag, Mongolia, during the 2001 Mongolian Academy of Sciences–American Museum of Natural History Paleontological Expedition. Little Ukhaa lies approximately 10 kilometers west of the main exposures at Ukhaa Tolgod. The Little Ukhaa locality was dis-

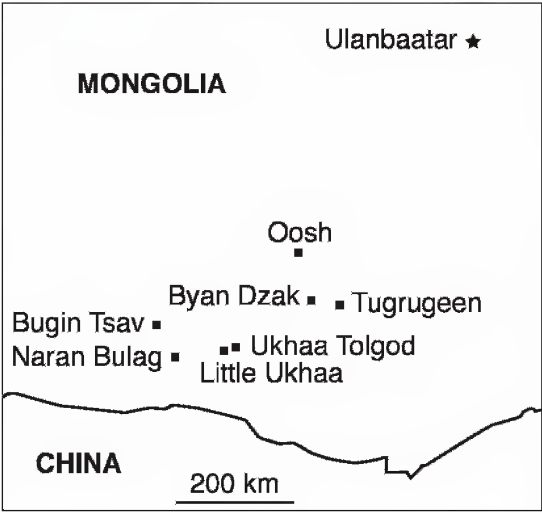


Fig. 1. Map showing the type locality in relation to other fossil localities in the Gobi Desert.

covered in 1996 (figs. 1, 2); it has produced a diverse assemblage of dinosaurs, lizards, and mammals and shares faunal similarity with Ukhaa Tolgod, but it may represent a slightly different age or environment due to the presence of *Bagaceratops* (a Barungoyotian protoceratopsian), which is unknown at the main Ukhaa Tolgod exposures. The geology and circumstances of vertebrate fossil occurrence at Ukhaa Tolgod has recently been reviewed by Loope et al. (1998) and Dingus et al. (in press). Basically, vertebrate fossils are most abundant in structureless sandstone facies, which have been interpreted as alluvial flows from catastrophically collapsing semistable sand dunes. Structural collapse was due to saturation of the dune. Several different alluvial flows have been identified at Ukhaa Tolgod, and this model has now been extended to Bayn Dzak (Dashzeveg et al., 2005). In many cases the remarkable preservation of specimens from Ukhaa Tolgod suggests that the animals were buried alive.

The age of the Ukhaa Tolgod fossil beds is not readily apparent. However, estimates based on faunal similarity to Bayn Dzak suggest a Campanian age (Dingus et al., in press).

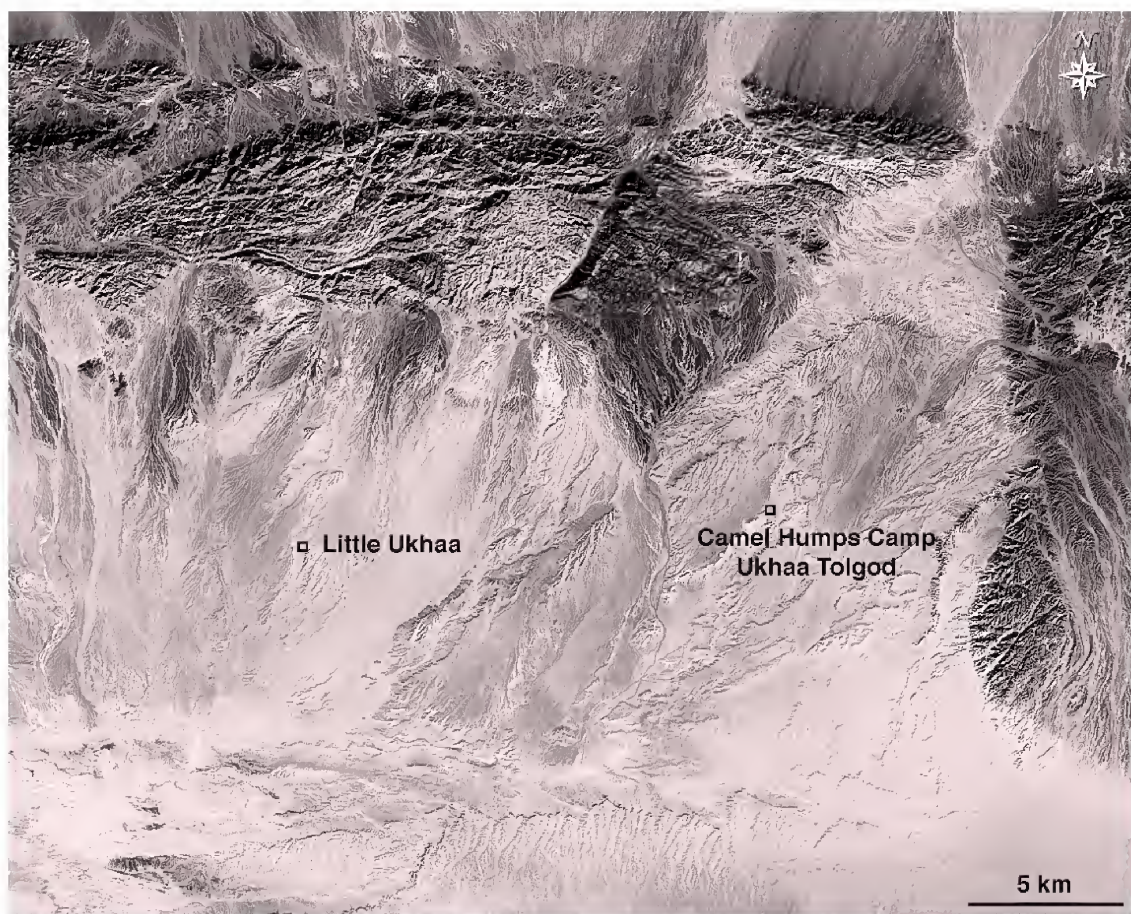


Fig. 2. The locality of Little Ukhaa showing its relationship to the main exposures at Ukhaa Tolgod, Omnogov, Mongolia.

SYSTEMATIC PALEONTOLOGY

SQUAMATA OPPEL, 1811
 ANGUIMORPHA FÜRBRINGER, 1900
 PLATYNOTA CAMP, 1923
 VARANOIDEA CAMP, 1923

Ovoo gurvel, new taxon

HOLOTYPE SPECIMEN: IGM 3/767, well-preserved partial skull with the braincase and mandibles missing.

ETYMOLOGY: *Ovoo-* is from Mongolian *ovoo* (pronunciation: *o-boe*), meaning “a heap or cairn” (fig. 3). A remnant of the pre-Buddhist religion of Mongolia, these cairns are said to be inhabited by local spirits. Occasionally they are also way points and

navigational aids along old caravan routes and, more recently, roads. *Ovoos* are venerated by Mongols and are worshipped by circling them clockwise three times and adding offerings in the form of rocks, prayer-flags, money and even vodka bottles. *Gurvel-* derives from the Mongolian word for lizard.

TYPE LOCALITY AND HORIZON: Little Ukhaa Tolgod Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Djadokhta Formation (Loope et al., 1998).

Known distribution: Known only from the type locality and horizon.

DIAGNOSIS: Distinguished from *Cherminotus longifrons* and other closely related varanoids by the following character states: nasals paired; presence of aperture between premaxilla



Fig. 3. A Mongolian *ovoo* at the spring of Naraan Bulag in the Nemegt Basin, Omnogov, Mongolia. 43° 27.891N 104° 57.84W

and maxilla (the premaxillary fenestra sensu Gauthier, 1982; see also Gao and Norell, 1998); anteromedial process of maxilla separating premaxilla from septomaxilla; dorsal septomaxillary foramen strongly reduced and close to midline (from Gao and Norell, 2000).

Sharing with *Aiolosaurus oriens* character states including presence of a premaxilla-maxilla aperture; dorsal septomaxillary foramen strongly reduced and close to midline. Distinguished from *Aiolosaurus oriens* and other closely related varanoids by the following derived character states: presence of paired mystery bones roofing the nasal/frontal suture; absence of dermal sculpturing on the skull bones (region unpreserved in *Aiolosaurus oriens*); premaxillary nasal process broader than deep; premaxilla-maxilla aperture large and rounded; premaxillary teeth 12 (as opposed to 7 in *Aiolosaurus oriens*); maxillary teeth 12–13 (*Aiolosaurus oriens* 10 at most).

DESCRIPTION

IGM 3/767 is composed of a rostrum and anterior postorbital region (fig. 4). The anterior wall of the orbit is preserved and the frontal is preserved to its contact with the parietal. Much of the suborbital bar is present, as is the left postorbital. Most of the palate is preserved in articulation, with vomers, ectopterygoids, and palatines preserved.

PREMAXILLA: The premaxillae are fused as a single element to form the anterior terminus of the snout. The nasal process is flat and straplike, and attenuates posteriorly as it divides the paired nasals by one half of the length of the process. Tiny posterior premaxillary foramina (anterior ethmoidal openings) are developed at the base of the nasal process. The tooth-bearing base of the premaxilla has a well-developed posterior shelf that forms an extensive subnarial floor ventral to the nasal process. The posterolateral border of the shelf is notched for the larger and rounded aperture between the premaxilla and maxilla, and the premaxilla contacts the maxilla at a loose fitting joint by its processes medial and lateral to the aperture. On the palate, a pair of short vomeromaxillary processes underlie the paired vomers. Adjacent to this contact is a single bilobate incisive process (fig. 4C). No ventral premaxillary foramina are observed; however, they may be obscured by replacement teeth. The fused premaxillae carry a total of 12 tooth positions, including seven functional teeth and empty spaces for five others. Eight replacement teeth are present at the bases of the functional teeth. This number of the premaxillary teeth is significantly different from that in *Aiolosaurus oriens*, which has a total of seven teeth from the type and only known specimen (Gao and Norell, 2000). The teeth are small, conical, and strongly recurved. The

premaxillary teeth are narrow laterally but slightly expanded labiolingually.

SEPTOMAXILLA: As in other varanoids, the septomaxillae are only visible in dorsal view. Together they form much of the floor of the narial chamber. Each septomaxilla is bulbous and is supported ventrally by the vomer and contacts the maxilla laterally. Medially a small ridge contacts the nasals just posterior to the nasal-premaxillary contact. Small dorsal septomaxillary foramina are present anteriorly in anteriorly projected troughs near the midline, lateral to the midline ridge.

NASAL: The paired, elongate nasals define the medial and posterior borders of the large retracted nares. Anteriorly, the tapering process of the nasal extends to a point along the contact with the nasal process of the premaxilla. The anterior process is roughly one half the length of the entire nasal bone. The narial border is crescentic but lacks anterolateral processes, and laterally the nasals have slight contact with the maxillae just posterior to the posterior corner of the nares. The lateral borders of the widened posterior halves of the nasals have short sutural contacts with the maxillae, but most of the lateral borders contacts the slender processes of paired mystery bones. As shown on the right side of the specimen, the posterior edge of the nasals overlaps the frontals beneath the "mystery bones" (fig. 5).

"MYSTERY BONES": The "mystery bones" are a pair of roofing elements otherwise unknown among squamates. The paired mystery bones overlie both the nasals and the frontals between the supraorbital processes of the prefrontals (fig. 5). This point is important because the nasals invariably overlie the frontal in squamates. Thus, the preserved condition demonstrates that the mystery bones are distinct from the anterior portions of the frontals that they overlie. They do not have any characteristics of osteoderms and are therefore neomorphic ossifications of the skull roof. The paired bones are relatively small thin plates, with a short midline suture contact. Anteriorly, each bone is bifurcated with a short anteromedial process along the midline, and a much longer anterolateral process extending between the nasal and the prefrontal. However, the latter process failed to reach

the retracted naris, allowing a short contact of the nasal with the maxilla. The lateral border of the mystery bone has a long sutural contact with the prefrontal, and this suture extends to the midlevel of the orbit. The medial border of the bone gradually curves posterolaterally from the midline, so that the bony plate is more or less triangular in shape with a short and rounded posterior process. Symmetry and the topological relationship of these structures with the surrounding bones testify to their identity as actual structures, not artifacts of preservation. To our knowledge, they have no known homolog among squamates or any other vertebrate clade.

FRONTAL: The paired frontals are subequal to the nasals in length. The dorsal surface of each bone is essentially smooth but is weakly ornamented with small longitudinal bumps and ridges along the posterior border. These appear to be related to the articular surface rather than dermal rugosities. A row of tiny irregular foramina extends from the midline anteriorly to adjacent to the orbital margin more posteriorly. The anterior third of the frontal is covered by the mystery bone, but as exposed on the right side, the frontal is anteriorly notched and slightly underlies the posterior border of the nasal beneath the mystery bone. The lateral border of the frontal contacts the elongate supraorbital process of the prefrontal along a longitudinal suture. For most of their length the lateral borders of the frontals are parallel sided; posteriorly, however, the borders curve laterally at the back of the orbit to form postorbital processes. The posterior third of the right frontal is broken and missing, but the left frontal is preserved to the simple and transverse frontal/parietal suture. The ventral surface is exposed enough to show the presence of extensive subolfactory processes (= cristae cranii, or frontal downgrowths), which meet at the midline as in extant *Varanus*. No bones of the skull table except for the postorbital (see below) are preserved posterior to the frontals.

MAXILLA: The subtriangular maxilla forms most of the lateral surface of the rostrum. The nasal process of the maxilla is low and not distinctly offset from the narial margin, such that the dorsal margin is a gentle, oblique incline in lateral view. The lateral surface of

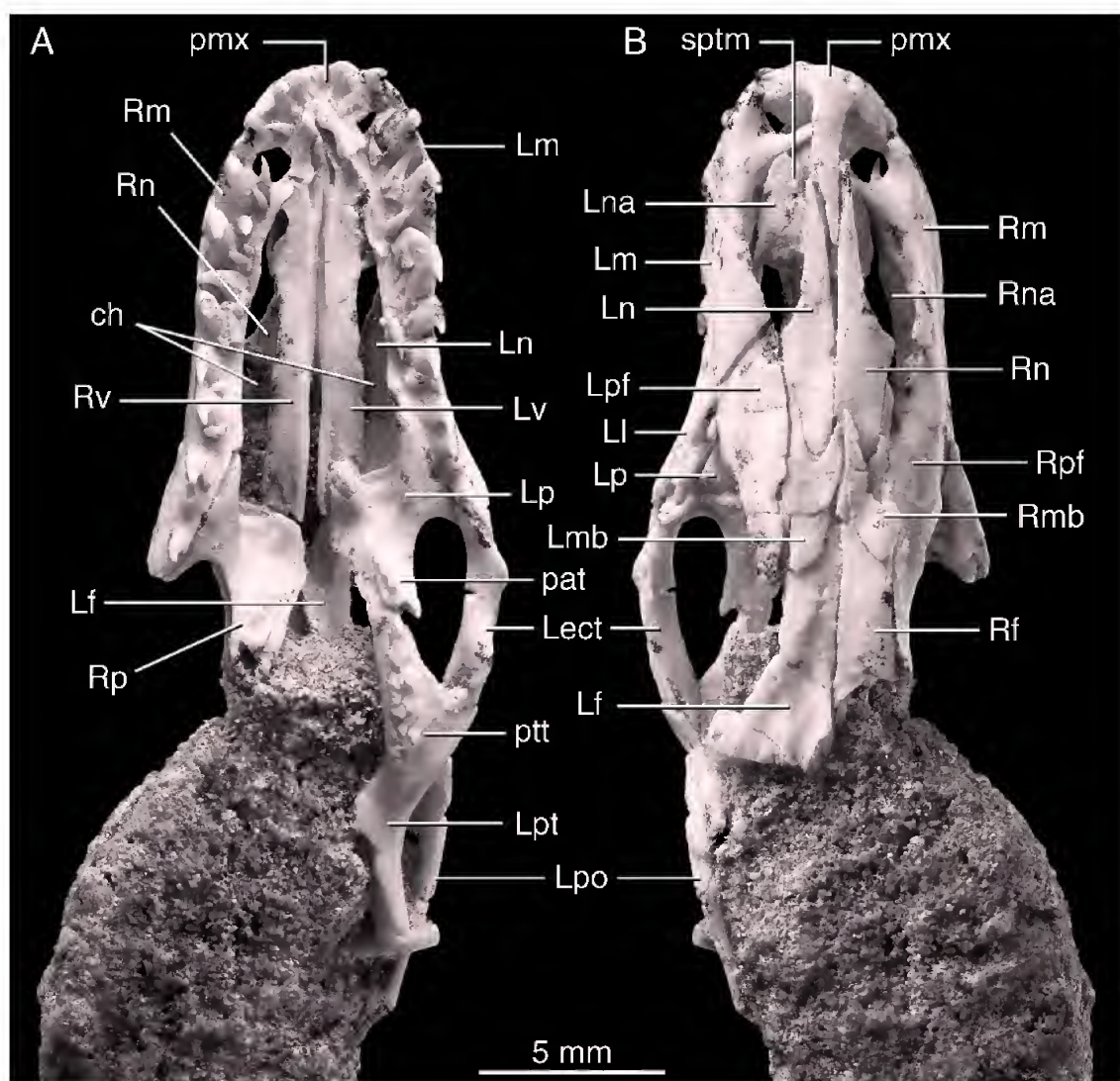


Fig. 4. A) The holotype skull of *Owoo gurval* in A, ventral, B, dorsal, C, left lateral, and D, right lateral views.

the maxilla shows a slightly impressed fossa posteriorly, bounded ventrally by the dental margin. A row of labial foramina (exits for the ethmoidal nerves and for labial blood vessels) parallels the dental border. In dorsal view, the bone is anteriorly forked with well-developed anterolateral (premaxillary) and anteromedial (septomaxillary) processes. Between these two anterior processes is a narial fossa and the semicircular notch for the large and rounded premaxillary aperture. The anteromedial process is anteroposteriorly short, but is medially elongate such that it contacts the opposite

process behind premaxillary nasal process. The narial margin starts anteriorly as a rounded ridge that becomes sharper and more medially curved posteriorly. Inside the narial chamber lie the well-ossified septomaxillae (see below), and lateral to the septomaxilla/maxilla contact is the anterior opening of the superior alveolar canal on the inner wall of the maxillary bone. The maxilla broadly overlaps the anterolateral surface of the prefrontal. The posterior suture between the nasal process and the prefrontal runs posterolaterally from the posterior terminus of the naris to the anterior

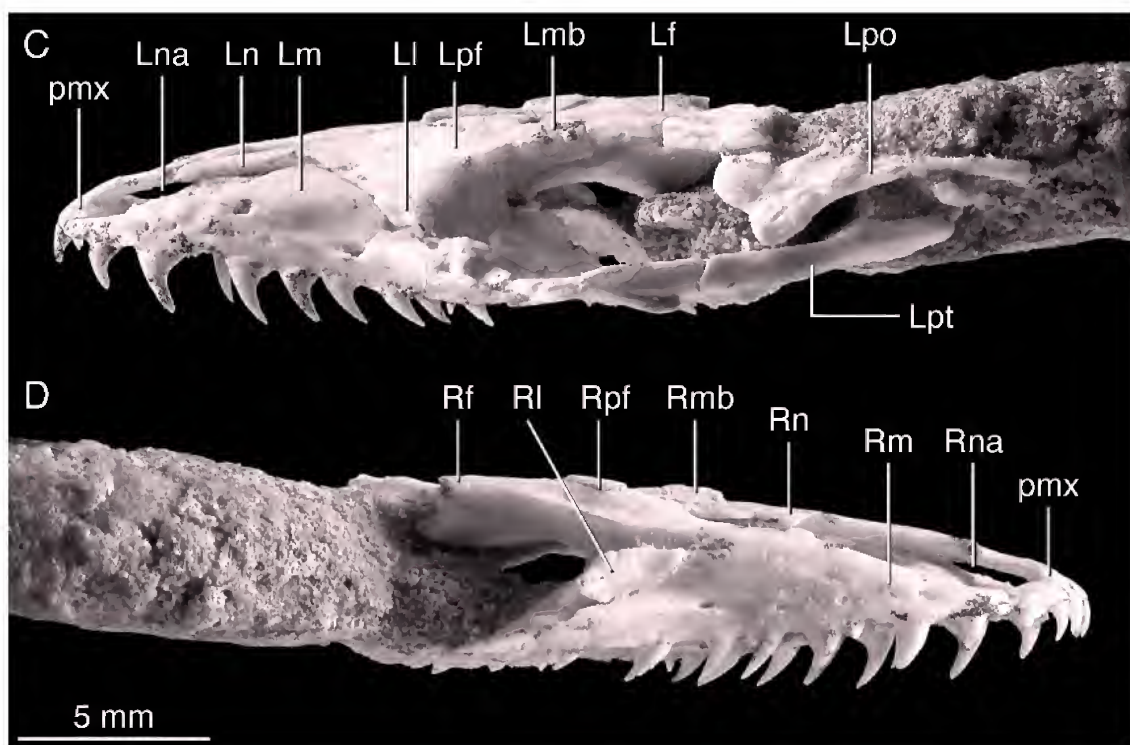


Fig. 4. Continued.

extremity of the orbit, where the maxilla contacts the small lacrimal (see below). The posterior process of the maxilla tapers posteroventrally. It contacts the lacrimal on the ventral surface of the latter, and lies on the lateral surface of the common contact between the palatine and ectopterygoid. The palatine-ectopterygoid contact occurs in about the anterior quarter of the orbit just posterior to the last maxillary tooth. Contact with the ectopterygoid is preserved on the left side of the skull and is a complex kinetic joint where the ectopterygoid fits into a socket formed by the maxilla ventrally and the palatine dorsally.

On the palatal surface, the maxillary teeth are supported by a narrow dental shelf, which borders the elongate internal choana. The dental shelf expands slightly medially posteriorly, reaching its widest point at the contact with the anterior terminus of the anterior maxillary process of the palatine. Posteriorly it contacts the palatine along a diagonal, laterally directed suture, which causes the skull to flare laterally at the anterior corner of the orbit. The posterior opening of the infraorbit-

al canal (maxillopalatine foramen) lies near this suture adjacent to the space between the penultimate and ultimate tooth. This opening of the infraorbital canal is most apparent on the left side, but it can also be observed on the right side.

The maxillary teeth have bases that are expanded anterodorsally and compressed laterally. The maxilla carries no more than 13 teeth for the complete tooth row; the left side shows 10 well-preserved teeth and the spaces for two to three others, and the right side has eight functional teeth and four to five empty spaces. The largest teeth are located anteriorly and in the middle portion of the tooth row, with posterior teeth progressively smaller. The maxillary teeth show weakly developed, but clearly defined infoldings at the tooth base. These are interpreted as plicidentine, a characteristic of extant varanoids (see Zaher and Rieppel, 1999, and Rieppel et al., 2003, for a discussion of this character). Along the maxillary tooth row lie several smaller replacement teeth at the base of the functional teeth, and these replacement teeth are approx-

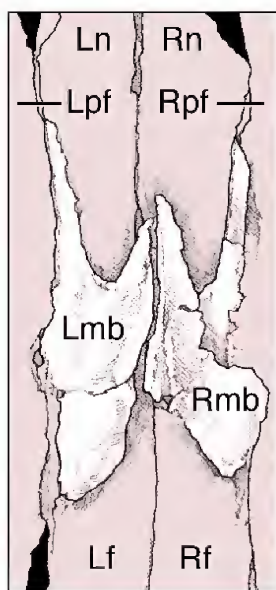


Fig. 5. Detail of the mystery bones.

imately half the size of, or even smaller than, the functional teeth. The teeth show well-developed resorption pits.

PREFRONTAL: The large prefrontal lies between the retracted nares and the orbits, and forms most of the anterior wall of the orbit. The frontal process of the prefrontal extends posteriorly to form most of the dorsal margin of the orbit. Although no contact is preserved between the prefrontal and the anterior process of the postorbitofrontal, a well-developed articular groove along the lateral edge of the frontals indicates that such a contact is present excluding the frontal from participation in the orbital margin. The orbital process of the prefrontal contacts the palatine in a broad suture that runs perpendicular to the long axis of the skull for most of its length, but is ventrolaterally directed near the lateral margin and extends posteriorly toward the jugal ventral to the lacrimal. The medial edge of this downward extension forms the lateral border of the orbitonasal fenestra and its lateral edge is notched to form the medial border of the dorsal posterior lacrimal foramen (fig. 6).

POSTORBITOFRONTAL: The postorbital and postfrontal are, apparently, fused in this taxon as they are in many extant *Varanus*, in contrast to the condition seen in the Eocene *Saniwa ensidens* (Rieppel and Grande, 2007).

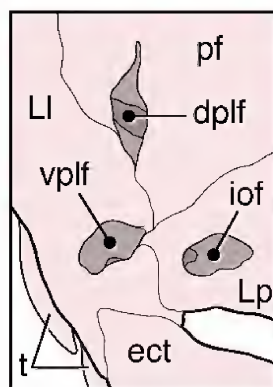


Fig. 6. The left anterior orbital wall.

A fragment of the postfrontal portion of the left postorbitofrontal is preserved adjacent to the frontal. The slender and elongate posterior process of the postorbital is completely preserved on the left side, and this process is still in articulation with the broken anterior process of the squamosal, demonstrating the presence of a complete supratemporal arch in this taxon. The anterior process (the frontal process of the postfrontal) of the postorbital bone is broken, but the articular groove along the lateral edge of the frontal indicates the presence of the prefrontal/postorbitofrontal contact as in some varanoids (e.g., *Cherminotus longifrons*, *Lanthanotus borneensis*, and *Varanus prisca*). The ventrolateral process of the postorbitofrontal is smooth, showing no indication of possible articulation with the (missing) jugal.

LACRIMAL AND POSTERIOR LACRIMAL FORAMINA: The lacrimal is nearly completely preserved on the right side of the skull but is fragmentary on the left. It is a small element, fitting in the anterior corner of the orbit, and contributes only to the lateral wall of the single lacrimal foramen (fig. 6). There is no pronounced, posterior flange like that seen in extant *Varanus*. The posterior lacrimal foramina are paired as in extant *Varanus* (see Norell et al., 1992: fig. 10). The dorsal posterior lacrimal foramen is relatively small, and opens between the prefrontal and the lacrimal, rather than penetrating the latter bone as in *Lanthanotus borneensis*. The ventral posterior lacrimal foramen is small and completely enclosed in the lacrimal. The jugal is not preserved on either side of the skull, but an

articular surface on the left ectopterygoid and a broken surface on the posterodorsal surface of the maxilla indicate its original presence in this taxon.

VOMER: The vomers are paired, greatly elongate and straplike, parallel-sided elements that lie adjacent to the midline of the palate. Anteriorly they contact the premaxilla and maxilla, and posteriorly they extend to contact the palatine at the level of the penultimate posterior maxillary tooth. Their lateral surface forms the entire medial boundary of the internal choana (*fenestra exochoanalis*). Anteriorly there is a small emargination just posterior to the contact with the maxilla, which presumably is the anterior opening for Jacobson's organ (*fenestra vomeronasalis externa*). Anteriorly the vomers meet and form a narrow fossa on the midline. At the anterior end of this fossa lies a pair of anteriorly projected vomero-premaxillary foramina. The vomers are in medial contact for only about half their length, being posteriorly separated by the so-called interpterygoid vacuity (or pyriform recess). Each vomer is L-shaped in cross-section. At their common anterior contact, they form a composite structure shaped like an inverted T in cross-section, where lateral flanges of bone form extensive vomerine shelves. The vomers are toothless as in other varanoids generally (but see *Eosaniwa koehni* [Rieppel et al., 2007]).

PALATINE: The palatines are paired, tetra-radiate elements. An anteromedial process of the palatine ventrally overlies the vomer in a broad overlapping joint (a scarf joint). A ventral tuberosity is present at the anterior margin of the palatine at the overlap with the vomer. A well-defined exochoanal fossa extends along the ventral surface of the palatine, but there is no development of a secondary palate. The exochoanal fossa possesses a thin roof divided by a lateral ridge at the posterior end as in *Lanthanotus borneensis*. The anterior maxillary process extends as a narrow splint to the level of the fourth-to-last maxillary tooth. Along the suture with the maxilla lies a small ventral opening from a branch of the infra-orbital canal. As mentioned above, the palatine with the maxilla forms a socket for articulation with the anterior process of the ectopterygoid. The large pterygoid process forms

slightly more than half of the medial boundary of the suborbital fenestra. The pterygoid contacts the palatine mostly medially where there is a groove to receive an anterolateral flange on the pterygoid. The pterygoid process and posterior/posterolateral margins of the maxillary process forms the anterior, and anteromedial boundary, of the suborbital fenestra. Anteriorly a small medial oblique surface projects into the pterygoid fenestra. A row of at least four small, conical, recurved palatine teeth are present beginning at the posterior margin of the palatine and extending forward (palatine teeth are lost in *Varanus* but are retained in some specimens of *Lanthanotus*, but see McDowell and Bogert, 1954; Jollie, 1960; Rieppel, 1980a).

PTERYGOID: The pterygoids are paired sinuous Y-shaped bones. Only the left pterygoid is well preserved. The ectopterygoid process is splintlike and fits into a deep laterally projected slot on the ectopterygoid. The laterally exposed surface of the pterygoid is dorsoventrally concave. On the ventral surface the ectopterygoid ramus is very short and forms none of the lateral border of the suborbital fenestra. The anteromedial (palatine) process carries a pair of loosely organized tooth rows that are anteriorly confluent with the palatine tooth row and that extend posterior to the midlevel between the suborbital fenestra and the basipterygoid process. Like the palatine dentition, the teeth are small but recurved and pointed. A transversely concave fossa laterally parallels this tooth row, originating just posterior to the level of the ectopterygoid process and extending posteriorly beyond the pterygoid teeth. Just posterior to the tooth row, the basipterygoid process projects medially and the thin, incomplete quadrate process extends posterolaterally.

ECTOPTERYGOID: Only the left ectopterygoid is completely preserved. It is a stout bone that bridges the palatine-maxilla complex with the pterygoid and forms the entire lateral boundary of the suborbital fenestra. In ventral view, the ectopterygoid arches laterally forming the widest part of the preserved region of the skull. The anterior process curves anteromedially to contact the palatine, excluding the maxilla from the suborbital fenestra. The ventral surface of the ectopterygoid is a nearly

flat to slightly concave surface. The ectopterygoid is apparently laterally exposed, but the dorsolateral surface was almost certainly overlain by the jugal (missing from the specimen; see above).

PALPEBRAL: No palpebral bones were found associated with IGM 3/767. However, in extant *Varanus* the palpebral lies in a slitlike fossa between the lacrimal and the prefrontal near the anterodorsal orbital rim. A well-defined fossa matching the *Varanus* condition is present in the new taxon, suggesting that a palpebral may have been present.

PHYLOGENETIC ANALYSIS

Phylogenetic relationships within the Varanoidea and, more globally, within the Platynota have been inferred from several semi-independent data sets (McDowell and Bogert, 1954; Borsuk-Bialynicka, 1983, 1984; Pregill et al., 1986; Norell et al., 1992; Norell and Gao, 1997; Lee, 1997; Lee and Caldwell, 2000; Rieppel, 2000). Recently, Conrad (in press) presented an extensive analysis of squamates based on morphological characters.

We added *Ovoo gurval* and 28 other taxa to the data matrix from Conrad (in press), which previously included 222 ingroup taxa and 363 morphological characters. The added taxa include eight species of *Varanus*, four recently described mosasaur species, two "agamids", two glyptosaurines, *Hymenosaurus clarki*, and 11 species-level codings to replace the previously compositely coded Iguanidae, Corytophanidae, Crotaphytidae, and Phrynosomatidae (see appendix 2). We also added 9 new characters to the data matrix. *Ovoo gurval* could be scored for 112 of the characters included in this new matrix. Character ordering and rationale were derived from Conrad (in press). We also corrected the codings for the *Varanus* species in that matrix to reflect the large contribution of the prefrontal to the orbitonasal fenestra. We also changed the coding to reflect the nature of the "crawling" sculpturing present on the skull bones of *Aiolosaurus oriens*. We analyzed these data using the computer program T.N.T. using the New Technology Search (1,000 replicates) and three subsequent ratchet replicates (each of 1,000 replicates). Our analysis

recovered 2288 equally short trees. The length of each tree is 3286 steps and a retention index of 0.7615.

We report both the strict consensus (fig. 7A) and the Adams consensus (fig. 7B) trees as recovered by PAUP* (Swofford, 2001). The Adams consensus collapses volatile taxa to their most basal recovered position and shows relationships that are consistent with all of the principle trees.

Ovoo gurval is recovered as a basal member of the Varaninae (those taxa closer to *Varanus varius* than to *Lanthanotus borneensis*) in all of the principal trees recovered in the T.N.T. analysis (fig. 7C–E). *Aiolosaurus oriens* is variably recovered as the sister taxon to *Cherminotus longifrons* (a derived lanthano-tine; Conrad, in press) (fig. 7C), as the basal-most member of Varaninae (fig. 7D), or as the sister taxon to *Ovoo gurval* at the base of Varaninae (fig. 7E). Consequently, the Adams consensus tree (fig. 7B) shows *Ovoo gurval* as the outgroup to *Saniwa ensidens* and *Varanus*. In the Adams consensus tree, Varanidae is supported by five unambiguous synapomorphies. These are: 3(1), presence of a rounded snout in dorsal view; 65(0), absence of a contact between the frontal and maxilla, and 149(1), laterally extensive crista tuberalis; 151(1), spheno-occipital tubercle placed anteriorly such that the crista tuberalis is posterodorsally inclined; and 178(0), presence of a ventrally convex dentary. The unambiguous synapomorphies supporting the clade formed by *Cherminotus longifrons* and *Lanthanotus borneensis* in the Adams consensus tree are: 32(1), presence of a medially flared palatine flange on the maxilla, and 83(1), presence of a nuchal fossa on the posterodorsal margin of the parietal. The clade consisting of *Ovoo gurval*, *Saniwa ensidens*, and *Varanus* is supported by 27(1), contact of the anteromedial processes of the maxilla posteroventral to the premaxillary nasal process; 51(1), absence of a contact between the jugal and postorbitofrontal; and 62(1), presence of a midline contact of the frontal subolfactory processes.

DISCUSSION

Ovoo gurval adds importantly to our knowledge of Djadoktha Formation squamates, to

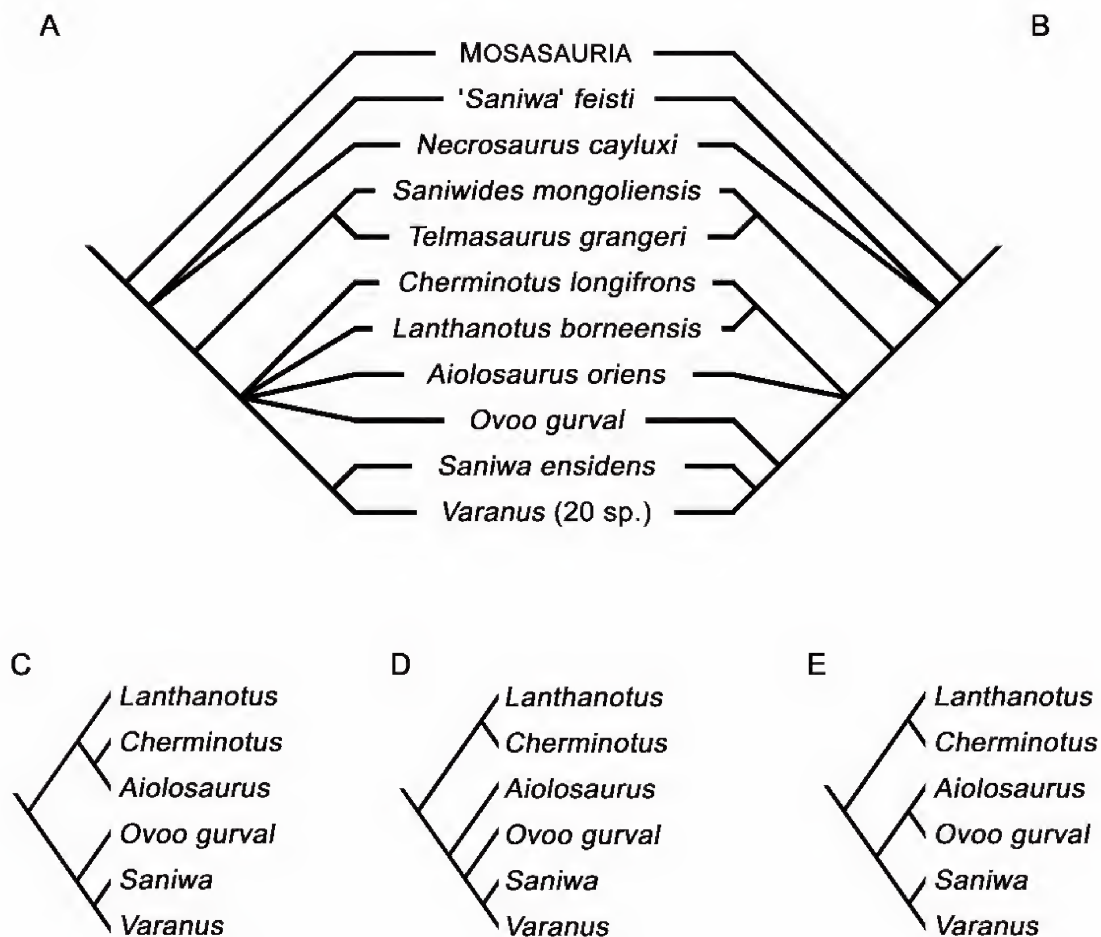


Fig. 7. A, strict consensus tree and B, the Adams consensus tree of the 2,288 most parsimonious trees. The length of each tree is 3,286 steps with a consistency index of 0.1493, and a retention index of 0.7615. C, D, and E, fundamental trees showing the differing placement of *Aiolosaurus oriens*.

known fossil squamate diversity, and to our understanding of varanid evolution. Many Djadoktha-aged platynotans have been discovered, but *Ovoo gurval* stands out because of its small size and its neomorphic mystery bones.

Ovoo gurval is the oldest known taxon that may be confidently referred to Varaninae and, as such, provides important details about the early evolution of varanines and varanids. *Cherminotus longifrons* was previously suggested as a possible relative of *Lanthanotus borneensis* (Borsuk-Bialynicka, 1984; Gao and Norell, 1998, 2000; Conrad, in press). Gao and Norell (1998) pointed out plesiomorphic features of *Cherminotus longifrons*, but the current analysis supports the placement of this

taxon as the sister to *Lanthanotus borneensis* based on several characters. More recently, *Aiolosaurus oriens* was also suggested as a possible lanthanotine based on characteristics not historically used to unite the group (Conrad, in press). Our inclusion here of *Ovoo gurval* into a data matrix derived from that presented by Conrad (in press) adds uncertainty about the position of *Aiolosaurus oriens* within Varanidae (fig. 7). Although some of this ambiguity may be the result of the incompleteness of the only known specimen of *Aiolosaurus oriens*, it may also be the result of recovering fossils that are increasingly close to the hypothetical ancestral form for Varanidae. If such is the case, then the observed (high) degree of similarity between

Aiolosauurs oriens, the basal varanine *Ovoogurval*, and the basal lanthanotine *Cherminotus longifrons* may suggest that the main varanid dichotomy occurred in the Late Cretaceous and that these three taxa may be very early relics from this initial radiation. By contrast, contemporaneous taxa that are often considered basal varanids (e.g., *Telmasaurus grangeri*, *Saniwides mongoliensis*) in fact fall outside the varanid crown (Borsuk-Bialynicka, 1984; Estes et al., 1988; Lee, 1998). Even so, they help to polarize basal character states for Varanidae. Importantly, they do not extend the minimum divergence time for the varanid clade or add to the potential missing lineage leading to crown Varanidae.

Extant varanids represent an astonishing range in size, five orders of magnitude, approaching the size range seen in extant terrestrial mammals (Pianka, 1995). The recently extinct "*Megalanias*" *prisca* further extends this range on the large end and was probably similar in mass to the largest terrestrial predators today. However, large size seems to have appeared relatively late within varanid lizards. Mesozoic varanids and members of the varanid lineage (varanoids exclusive of monstersaurs and mosasauroids) are all relatively small. *Ovoogurval* is among the smallest varanids known, approaching the size of small extant *Odatria* species today, such as *Varanus* ("*Odatria*") *brevicauda*. Consequently, it helps reconstruct Varanidae as coming from relatively small ancestral forms. *Ovoogurval* also helps to demonstrate that varanid skull morphology has remained remarkably conservative despite the vast range in size that has evolved since the Cretaceous.

Preservation of the two neomorphic elements on the dorsal surface of the skull also speaks to the importance of *Ovoogurval* among fossil squamates. These elements look nothing like the rounded, domelike osteoderms of many basal varanoids and extant *Heloderma*. Nor do they resemble the platelike osteoderms seen in many extant anguids or the wormlike structures of some *Varanus*. They are generally very similar to the dermal skull roofing bones of other squamates, but share no apparent homology among those roofing bones. These elements hint at an unknown

developmental mechanism that may have duplicated the anterior parts of the frontals in *Ovoogurval*.

ACKNOWLEDGEMENTS

We thank Amy Davidson for preparation of the extremely delicate specimen and Mick Ellison for photography. Members of the 2001 Mongolian Academy of Sciences–American Museum of Natural History field crews are thanked for working so hard while they had so much fun. The manuscript benefited from careful review by two anonymous reviewers. This research was supported by the Carter Fund and the Kalbfleisch Fund at the American Museum of Natural History.

REFERENCES

- Ast, J.C. 2001. Mitochondrial DNA evidence and evolution in Varanoidea (Squamata). *Cladistics* 17: 211–226.
- Augé, M., and R.M. Sullivan. 2006. A new genus, *Paraplaosauriops* (Squamata, Anguinae, Glyptosaurinae), from the Eocene of France. *Journal of Vertebrate Paleontology* 26: 133–137.
- Bell, G.L., Jr., and M.J. Polcyn. 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the Middle Turonian of Texas and comments on the phylogeny of Mosasauridae (Squamata). *Netherlands Journal of Geosciences* 84: 177–194.
- Bellairs, A. 1970. *The Life of Reptiles*. New York: Universe Books, 1, 590 pp.
- Borsuk-Bialynicka, M. 1983. The early phylogeny of Anguimorpha as implicated by craniological data. *Palaeontologica* 28: 1–42.
- Borsuk-Bialynicka, M. 1984. Anguimorphans and related lizards from the Late Cretaceous of the Gobi Desert. *Palaeontologia Polonica* 46: 5–105.
- Camp, C.L. 1923. Classification of the lizards. *Bulletin of the American Museum of Natural History* 48: 289–481.
- Clos, L.M. 1995. A new species of *Varanus* (Reptilia, Sauria) from the Miocene of Kenya. *Journal of Vertebrate Paleontology* 15: 254–267.
- Conrad, J.L. in press. Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bulletin of the American Museum of Natural History*.
- Conrad, J.L., and M.A. Norell. 2006. High-resolution x-ray computed tomography of an Early Cretaceous gekkonomorph (Squamata)

- from Öösh (Övörkhangai; Mongolia). *Historical Biology* 18: 405–431.
- Conrad, J.L., and M. Norell. 2007. A Complete Late Cretaceous Iguanian (Squamata, Reptilia) from the Gobi and Identification of a New Iguanian Clade. *American Museum Novitates* 3584: 1–47.
- Conrad, J.L., O. Rieppel, and L. Grande. In press. An Eocene iguanian (Squamata: Reptilia) from Wyoming, U.S.A. *Journal of Paleontology*.
- Dashzeveg, D., L. Dingus, D.B. Loope, C.C. Swisher, III, T. Dulam, and M.R. Sweeney. 2005. New stratigraphic subdivision, depositional environment, and age estimate for the Upper Cretaceous Djadokhta Formation, southern Ulan Nur Basin, Mongolia. *American Museum Novitates* 3498: 1–31.
- Dashzeveg, D., M.J. Novacek, M.A. Norell, J.M. Clark, L.M. Chiappe, A. Davidson, M.C. McKenna, L. Dingus, C. Swisher, and P. Altangerel. 1995. Extraordinary preservation in a new vertebrate assemblage from the Late Cretaceous of Mongolia. *Nature* 374: 446–449.
- de Queiroz, K., C. Ling-Ru, and J.B. Losos. 1998. A second *Anolis* lizard in Dominican amber and the systematics and ecological morphology of Dominican amber anoles. *American Museum Novitates* 3249: 1–23.
- Dingus, L., D.B. Loope, D. Dashzeveg, C.C. Swisher, III, C. Minjin, M.J. Novacek, and M.A. Norell. In press. The geology of Ukhaa Tolgod (Djadokhta Formation, Upper Cretaceous, Nemegt Basin, Mongolia). *American Museum Novitates*.
- Erickson, G.M., A. de Ricqlès, V. de Buffrénil, R.E. Molnar, and M.K. Bayless. 2003. Vermiform bones and the evolution of gigantism in *Megalia*—how a reptilian fox became a lion. *Journal of Vertebrate Paleontology* 23: 966–970.
- Estes, R. 1983. *Sauria terrestria*, *Amphisbaenia*. New York: Gustav Fischer Verlag, 249 pp.
- Estes, R., K. de Queiroz, and J. Gauthier. 1988. Phylogenetic relationships within Squamata. In R. Estes and G. Pregill (editors), *Phylogenetic relationships of the lizard families*: 119–281. Stanford, CA: Stanford University Press.
- Fuller, S., P. Baverstock, and D. King. 1998. Biogeographic origins of goannas (Varanidae): a molecular perspective. *Molecular Phylogenetics and Evolution* 9: 294–307.
- Fürbringer, M. 1900. Zur vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln. *Jenaische Zeitschrift für Naturwissenschaft* 34: 215–718.
- Gao, K.-Q., and M.A. Norell. 1998. Taxonomic revision of *Carusia* (Reptilia: Squamata) from the Late Cretaceous of the Gobi Desert and phylogenetic relationships of anguimorph lizards. *American Museum Novitates* 3230: 1–51.
- Gao, K.-Q., and M.A. Norell. 2000. Taxonomic composition and systematics of Late Cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities, Mongolian Gobi Desert. *Bulletin of the American Museum of Natural History* 249: 1–118.
- Gauthier, J.A. 1982. Fossil xenosaurid and anguid lizards from the early Eocene Wasatch Formation, southeast Wyoming, and a revision of the Anguioidea. *Contributions to Geology University of Wyoming* 21: 7–54.
- Goloboff, P.A., J.S. Farris, and K. Nixon. 2003. TNT: tree analysis using new technologies. Program and documentation available from the authors and at <http://www.zmuc.dk/public/phylogeny>.
- Haber, A., and M.J. Polcyn. 2005. A new marine varanoid from the Cenomanian of the Middle East. *Netherlands Journal of Geosciences* 84: 247–255.
- Hecht, M.K. 1975. The morphology and relationships of the largest known terrestrial lizard, *Megalia prisca* Owen, from the Pleistocene of Australia. *Proceedings of the Royal Society of Victoria* 87: 239–249.
- Jollie, M.T. 1960. The head skeleton of the lizard. *Acta Zoologica* 41: 1–64.
- Lazell, J.D., Jr. 1965. An *Anolis* (Sauria, Iguanidae) in amber. *Journal of Paleontology* 39: 379–382.
- Lee, M.S.Y. 1995. Possible affinities between *Varanus giganteus* and *Megalia prisca*. *Memoirs of the Queensland Museum* 39: 232.
- Lee, M.S.Y. 1997. The phylogeny of varanoid lizards and the affinities of snakes. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 352: 53–91.
- Lee, M.S.Y., and M.W. Caldwell. 2000. *Adriosaurus* and the affinities of mosasauroids, dolichosaurs, and snakes. *Journal of Paleontology* 74: 915–937.
- Loope, D.B.L. Dingus, C.C. Swisher, III, and C. Minjin. 1998. Life and death in a Late Cretaceous dune field, Nemegt Basin, Mongolia. *Geology* 26(1): 27–30.
- Makovicky, P.J., M.A. Norell, J.M. Clark, and T. Rowe. 2003. Osteology of *Byronosaurus jaffei* (Theropoda: Troodontidae). *American Museum Novitates* 3402: 1–21.
- McDowell, S.B., and C.M. Bogert. 1954. The systematic position of *Lanthanotus* and the affinities of anguimorph lizards. *Bulletin of the American Museum of Natural History* 105: 1–141.

- Mertens, R. 1942. Die Familie der Warane (Varanidae). Zweiter Teil: Der Schädel. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 465: 117–234.
- Molnar, R.E. 2004. Dragons in the dust: the paleobiology of the giant monitor lizard *Megalania*. Bloomington: Indiana University Press, 211 pp.
- Norell, M.A. 2004. *Estesia mongoliensis*. In E. Pianka and D. King (editors), Varanoid lizards of the world. Bloomington: Indiana University Press: 539–541.
- Norell, M.A., and K.-Q. Gao. 1997. Braincase and phylogenetic relationships of *Estesia mongoliensis* from the Late Cretaceous of the Gobi Desert and the recognition of a new clade of lizards. American Museum Novitates 3211: 1–25.
- Norell, M.A., M.C. McKenna, and M.J. Novacek. 1992. *Estesia mongoliensis*, a new fossil varanoid from the Cretaceous Barun Goyot Formation of Mongolia. American Museum Novitates 3045: 1–24.
- Oppel, M. 1811. Die Ordnungen, Familien und Gattungen der Reptilien als Prodom einer Naturgeschichte derselben. München: Joseph Lindauer Verlag.
- Páramo, M.E. 1994. Posición sistemática de un reptil marino con base en los restos fósiles encontrados en capas del Cretácico superior en Yaguará (Huila). Revista de la Academia Colombiana de Ciencias Exactas Físicas y Naturales 19: 63–80.
- Páramo-Fonseca, M.E. 2000. *Yaguarasaurus columbianus* (Reptilia, Mosasauridae), a primitive mosasaur from the Turonian (Upper Cretaceous of Colombia. Historical Biology 14: 121–131.
- Pepin, D.J. 2001. Natural history of monitor (family Varanidae) with evidence from phylogeny, ecology, life history and morphology. Ph.D. dissertation, Washington University, St. Louis, MO, 234 pp.
- Pianka, E.R. 1995. Evolution of body size: varanid lizards as a model system. American Naturalist 146: 398–414.
- Polcyn, M.J., and G.L. Bell, Jr. 2005. *Russellosaurus coheni* n. gen., n. sp., a 92 million-year-old mosasaur from Texas (USA), and the definition of the parafamily Russellosaurina. Netherlands Journal of Geosciences 84: 321–333.
- Pregill, G.K., J.A. Gauthier, and H.W. Greene. 1986. The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. Transactions of the San Diego Society of Natural History 21: 167–202.
- Rieppel, O. 1980a. The phylogeny of anguino-morph lizards. Denkschriften der Schweizerischen Naturforschenden Gesellschaft 94: 1–86.
- Rieppel, O. 1980b. Green anole in Dominican amber. Nature 286: 486–487.
- Rieppel, O., J.L. Conrad, and J.A. Maisano. 2007. New morphological data for *Eosaniwa koehni* Haubold 1977 and a revised phylogenetic analysis. Journal of Paleontology 81(4): 760–769.
- Rieppel, O., and L. Grande. 2007. The anatomy of the fossil varanid lizard *Saniwa ensidens* Leidy, 1870, based on a newly discovered complete skeleton. Journal of Paleontology 81(4): 643–665.
- Rieppel, O., and H. Zaher. 2000. The intramandibular joint in squamates, and the phylogenetic relationships of the fossil snake *Pachyrhachis problematicus* Haas. Fieldiana Geology New Series 43: 1–69.
- Rieppel, O., H. Zaher, E. Tchernov, and M.J. Polcyn. 2003. The anatomy and relationships of *Haasiophis terrasanctus*, a fossil snake with well-developed hind limbs from the Mid-Cretaceous of the Middle East. Journal of Paleontology 77(3): 536–558.
- Sullivan, R.M., and M. Augé. 2006. Redescription of the holotype of *Placosaurus rugosus* Gervais 1848–1852 (Squamata, Anguidae, Glyptosaurinae) from the Eocene of France and a revision of the genus. Journal of Vertebrate Paleontology 26: 127–132.
- Swofford, D.L. 2001. PAUP* Beta 10 Software. Sunderland, MA: Sinauer Associates.
- Uetz, P. 2007. The EMBL reptile database. Heidelberg: European Molecular Biology Laboratory, <http://www.reptile-database.org>
- Zaher, H., and O. Rieppel. 1999. Tooth implantation and replacement in squamates, with special reference to mosasaur lizards and snakes. American Museum Novitates 3271: 1–19.

APPENDIX 1

CODINGS FOR ADDED TAXA

Here we offer the codings for all species of *Varanus* used in this analysis and for the added taxa from Iguania, Scincomorpha, and Glyptosaurinae (totaling 30 added species). Note that these codings may be cut from the (free) pdf available <http://digitallibrary.amnh.org/dspace/> and added to the matrix of Conrad (in press) available from the same website. Note that added taxon names are followed by specimens used to help in coding them. Soft-tissue characters are coded from the literature. Further explanation of character codings are found in Conrad (in press).

[*Varanus*—eight added species, 20 species total]

Varanus acanthurus [FMNH 98935; FMNH 218083]

1100010001?10000100001300111101110000?001111
00110012?1002000110?0000110211010?0000000001
100011021001100?1011100100101210000101000000
000021?100100010101010000011?000000001101000
000001120?00010100110001000?1011011202001100
201000???12022021?01121101000002110010001111
002000010200000?100120000001?00?1?10000?????
01000???
0000210

Varanus bengalensis [FMNH 22495; AMNH R-117786; AMNH R-118714]

310001?000120000000101300101001010000?001111
00110012?1002000110?00001102100100?01}001000
001100010011001100?1011111100101210000101000
0000000200110000010101010000011?10000000?00
000000001020?0001011011000?00?1011011202001
10020100011012022021?00121101000002110010001
110002000000200000?100110000000?00?1?10000??
????00000????0????????????????????????????????
??000000010

Varanus dumerilii [FMNH 223194; FMNH 228151]

2100010001110000100101200111001010000?001111
00110012?1002000110?000011011001000000110101
100021031001100?1011111100101210000101010002
00002??0{01}0000010101010000011?00000000?000
00000001120?0001011011000?00?10110112020011
00201000???12022021?011211010000021100100011
11002000010200000?100120000000?00?1?10000????
??01000????0??????????????????????????????????
000000?10

Varanus eremius [Mertens, 1942]

110001?000120000100001300111001010000?001111
00110?12?1002000110?000011021101000000000201
100011021001100?10111001001012100001010?0000
00002?0?0?0?10101010000011?1000000011010000
00001120?00110110110001000?10010112020011002
01000???120?2021???2?10100?0021100?00011?002
0000??200000?100??0000?0000?1?10000?0?00?000

00????0????????????????????????????????????0000?
0210

Varanus exanthematicus [AMNH R-140801; FMNH 212985]

1100010001120000000111300101101010000?001111
00110011?1002000110?000011021101000000{01}00
001100011011001100?1011101100101210000101010
00000002001101000101010100000112000000001101
000000001120?00010110110001000?1001011502001
10020100011012022021?02121101000002110010001
1100020000?0200000?1001100000000000?1?10000?0
?00?00000????0????????????????????????????????
???000010220

Varanus flavescens [AMNH R-77646]

210001?000120000000101300101101010000?001111
0011{01}011?1002000110?000011021101000000000
001100011021001100?1011101100101210000101000
00000002001100100101010100???11?100000001101
000000001120?00010110110001?00?1001011202001
100201000???12012021?0112110100000211001000?1
1?00?0000???000000?1001100000?1?00?1?10000????
?00000?0???0??????????????????????????????????
000?0210

Varanus gouldii [FMNH 250434]

3100010001120000100101300111101010000?001111
00110?12?1002100110?000011021111000001000001
100011021001100?1011100100101210000101000000
0000200110000010101010000011?100000001101000
000001120?00010110110001000?1001011202001100
201000???12022021?01121101000002110010001110
002000010200000?1000200000010000?1?10000?0?00
?01000????0??????????????????????????2??????????
000000210

Varanus griseus [AMNH R-47726; AMNH R-47725; FMNH 17142; FMNH 22354]

2100010001120000100101300101001010000?001111
00110011?1002000110?000011011101000001000001
100011021001100?1011101100101210000101010000
00002001?01000101010100000112000000001101000
000001120?0001010011?001000?1001011202001100
201000110120?2021?01121101000002110010001110

0020000?0200000?1001100000000000?1?100001010
0?00000?4111010101???21101?001121?11112???????
???????0?0?0?0220

Varanus indicus [AMNH R-58389; AMNH R-142623]

210001000111{01}000100{01}01300111101{01}100
00?00111100110?12?1002100110?000011021101000
000100001100011021001100?1011101100101210000
1010000000000210?10000010101010000011?100000
00110{01}00000001020?00010110110001000?1001
011202001100201000???12012021?01121101000002
1100?0001111002000000200000?1001100000000000
?1?10000?0?00?00000?000?0?0?0?0?0?0?0?0?0?0?
0?
000010210

Varanus komodoensis [AMNH R-37908; FMNH 22198; FMNH 22199]

3110010001120000100101300111101110000?001111
0011001{12}?1002000110?000011011101000001000
001100011021001100?1011100100101210000101000
00000002001100000101010100000112100000001100
000000001120?00110110110001000?1001011202001
10020100011012022021?011211010000021100100??
11?0020000??000000?1001100000?0?00?1?10000?0?
00300000?0??0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?
?000?0200

Varanus kordensis [Mertens, 1942]

2100010001110000100011300111101110000?001111
00110?12?1002000110?000011011101000000000001
100011011001100?1011100100101210000101000000
0000210?0?100?101010100??11?1000000011010?00
0001?20?00?0110110001?00?1001011202001100201
0001???
????????????????00?1?10000?00001000?000?0?0?0?
????????????????????????????????0?00?0210

Varanus niloticus [AMNH R-74603, AMNH R-10524; FMNH 22084; FMNH 17145]

2100010001120000100111300101101010000?001111
00110011?1002000110?000011021101000001000001
100011021001100?10111011001012100000101010000
000021?1101000101010100000112100000001101000
000001120?00010110110001000?1001011512001100
20100011012012021?01121101000002110010001110
012000000200000?1001100000000000?1?10000?0?00
?00000?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?
00010220

Varanus olivaceus [FMNH 223181]

2100010001110000100101300111101010000?001111
00010?12?1001000110?000011021111000001000001
100011021001100?1011101100101210000201010000
0000200?0000?10101010000011?00000000?010000

00001120?00010110110001000?10110105120011002
01000???120?2021????2?10100?0021100?00011??002
0000??200000?100??0000?0000?1?10000?0?00?000
00????0?0????????????????????????????????0?00?
0210

Varanus prasinus [FMNH 229907]

2100010001110000100011300111101110000?01111
00110?12?1002000110?000011011101000000100001
100011021001100?1011100100101210000101000000
000021?100100010101010000011?000000001101000
000001120?00?011011?00????????????????00?
???1201202?001????????????0111000?????000
00?10011000??1?00?1?10000????00000????0????
????????????????????????????000010210

Varanus prisca ("Megalania" prisca) [AMNH FR-6302; Hecht, 1975; Lee, 1995; Erickson et al., 2003; Molnar, 2004]

?11???00?1????01????3001?11?1????1????????????
??002120110?00001011110000??0?0011?0?0?????
????????0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?
????????0?1?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?
2020011002?000???120220?1???1???010?00021100??
????????000?000?0?0?0?0?0?0?0?0?0?0?0?0?0?0?
0?
?0?0?

Varanus rusingensis [Clos, 1995]

?????????????????????1?11?01?????????????????
????????????0210010000?0?0?0?0?0?0?0?0?0?0?
???
00?0???10?000001?20?0?0?0?0?0?0?0?0?0?0?0?
2001100??000???120120?1???1???010000021?00?0??
11?00?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?
????????????000?000?1?0000?1?????????????????
???
???

Varanus salvadorii [AMNH R-59873]

3110010001120000100001300111101110000?001111
00110012?10021{01}0110?00000101110100000{01}
000001100011011001100?1011100100101210000101
000000000021?1000000101010100000112100000001
100000000001120?00110110110001000?1011011202
001100201000110120220?0001?1?0?0?0?0?0?0?0?
????????00?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?
00????0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?
0200

Varanus semiremex [Mertens, 1942]

2110010001110000100001300111101010000?01111
00110?12?1002000110?000011011101000000000001
100011021001100?10111001001012100001010?0000
00002?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?0?
00001120?00110110110001000?10010112020011002

01000???120?2021????2?10100?0021100?00011??002
0000??200000?100??0000??0000?1?10000?0?00?010
00????0????????????????????????????????0000?
0210

Varanus tristis [Mertens, 1942]

2100010001111000100011300111101010000?011110
0?10?12?1002000110?0000110111010000000000011
00011011001100?10111001001012100001010?00000
0002?0?0?00?10101010000011?100000001101000000
001120?00010110110001000?10010112020011002010
00???120?2021????2?10100?0021100?00011??0020000
??200000?100??0000?0000?1?10000?0?00?01000???
?0????????????????????????????????0000? 0210

Varanus varius [Mertens, 1942]

3110010001120000100101300111101010000?001111
00110?12?1002100110?000011011101000000000001
100011021001100?101111100101210000101000000
000021?1100000101010100000112100000001101000
000001120?00110110110001000?1001011202001100
201000? ??????????????????????????????????????
0000?100???000?1??00?1?10000????0000?0???0???
????????????????????????????????0???0100

[Iguania—15 species]

Aciprion formosum [AMNH FR-1609]

0000?10001110?0000000030?0?000?010?0?010??00
0110010110200????0?0?0101?012?00?000001??1?1
?011000? ??????????????????????????????????????
?????????1??00? ???????0?010?210000?1110?0?00
??0??00??00400000000000000? ??????????????????
???
???
?????????

Basiliscus basiliscus [AMNH R-75615; AMNH R-57769]

10000100011100000000003001100000010000001000
00011001111021010?0?0000010121110?010?00001
001???0200000000010000001000111101000000000
0001000000100010000000000010?00000000?00000
01002032110011010010?00?00?0000200400000000
00000000012100001?010?0101000002000010010100
000000000100000?100010000001010???0000?0?????
?0000?1???0????????????????????????????????0?
0010001

Callisaurus draconoides [AMNH R-14780; AMNH R-147841]

001000?0001100000000103101000001010000101000
00110001111020000?0?010011111201201000100001
10011000000000011000100010100211110300000000
000001?100100010000000000011?00000000?00101

01012032100011010010?000000?0010000300000000
00000000012000101?0100110100000100001?000100
011000011100100?100010000001??0??1?100?00?0???
0?00001??0?0????????00? ??????????????????????
?0000000

Corytophanes hernandesii [AMNH R-147880]

0000000011110000000010?101100001010001001000
00011100111021010?0?00000100121110?001?00001
101???02000000001000100010100111101000000000
000001?100100010000000000011?00000000??00000
01002032100011011010?000000?0000200400000000
00000000012000001?10000101000002000000000100
000000000100000?100110000001010???000?00?0???
??000?1???0????????01?????????????????????????
?0010?02

Crotaphytus bicinctores [AMNH R-108970; AMNH R-108972]

0000000011110000000003001000001010000101000
00000101111021000?0?0000010112002000001000010
10100010000000011000100000101{02}110010010000
000001000000000110000000000011200000000??0{01}
11?01002032110001011010000000?000020040000000
000100000012000001?10001101000002000000001110
010000001100000?1000100000010?0001?100000?0???
?000?100000?00?0?0?01?????????????????????????
0000200

Crotaphytus collaris [AMNH R-2363; AMNH R-84489; AMNH R-69060]

0000000111110000000010300100000101000010100
000100101111021000?0?00000101120020000010000
10101000100000001100010000010111110000100000
00001000000000010000000000011?00000000?0010
101001032110011011010?000000?000020040000000
000100000012000001?1000110100000200000?00111
0010000010100000?100010000001??0???100?00?0??
???000?10000?0?0????01????????????2????????????
?000000100

Gambelia wislizenii [AMNH R-147874; AMNH R-147875]

100000?0001100000000003{01}00?01001010000101
00000100001111021000?0?000001011200200000100
00101010001000000011000100010101111100001000
0000001000000200010000000000011?00000000?00
10101002032110010011010?000000?0000200400000
00000100000012000001?1000110100000200000?010
11001000001110000?100010000001??0???100?00?0
???000010000? ?????????????????????2????????????
?000000000

Hydrosaurus amboiensis [AMNH R-140825]

100001?0001100000000013010?01000010000101010
00001000111020000?0?100011011011220001000001

0001100200000000000010000010121110000000000
0001000000100010100000000011?00000000?02001
010101320?0011010010?000000?0000100101100000
?03000000121010?1?100?01010010020000?0001000
11000000100000?100110000001?0?0?1?00?????????
000????0????????????????????????????????????000
000200

Microlophus albermarlensis [AMNH R-77624]

000000?0001100000000101000?010010100000010000
0010001011021000?0?00000101100020000020000110
01100100000001100010000010011110000001000000
000001001?00100000001?0011?00000000?02101010
020120?00100100100000?00?00002004000000000000
00???12000001?100?1101000001000010?01110011000
011100000???01000000???1???000?0?????????0?1??
0????????????????????????????????????0?0??? 00

Petrosaurus mearnsi [AMNH R-141107; AMNH R-60513]

101000?0001100000000003111100001010000101000
00100001011021000?0?{01}1001111200220000000
001100100010000000010001000101002111000000{0
1}0000000101?100000010000000000011?00000000?
?0010100002032100010011010?000000?0010000400
00000000000000012000001?000?110100000100000?
001100001000011100100?100010000001?0?0?1?100?
00?0???0?000?1???0?????????????????????????????
?????0?0100200

Phrynosoma asio [AMNH R-72636; AMNH R-74838]

10010020111100000000101110?00001010000101000
00111101111021000?0?0000010012002011?100011?
020101000000000110001000101002000000000{01}0
000000001?10010001000000000001?00000000?00
10000010032120011010010?100010?1001200300000
0000000000012001101?1000110100000200001?0101
00000000021200200?100120000001?0?0?1?100?00?0?
?0?00001?0?0?????????????????????????????????
000?00?00

Plica plica [AMNH R-85313; AMNH R-141159]

000000?0001100000000103101100001010000001000
00111000111021000?0?00001111200200000100001
10011001000000010000100000100211101000000000
000101?100100010000000000011?00000000?03001
000120320?01???11010?000000?00002004000000000
0100000012000001?110011010000010000100001100
11000011100000?100020000001?0?0???000?00?0????
000?1???0????????????????????01????????????0?
000200

Pogona barbata [AMNH R-76196; AMNH R-76570]

00000120011000000000103010?01000010000003??1
00001000111020000?0?000011011201200000000001
011???02000000000000100000100211111000000000

000100010010001000000000011?00000000?02000
00010132110011010010?00?00?0000200101100000?
00000?012001001?0000010100000200001?0101000
01000011100000?100110000021??0?1?10?0?????????
000????0????????????????????????????????????000
010000

Sceloporus olivaceus [AMNH R-93186; AMNH R-93183]

1010000011120000000010300100000101000010100
000000001011021000?0?10000101120020000020020
11101000100000000100010001010020000000101000
00001000000100010000000000011?00000000?0010
1000010121100000100100000000?000020030000000
000000000012000101?1100110100000100001?01111
0011000011100000?100020000001?1?1?1?100?00?0?
?0?000?1???0?????????????????????????????????
00000200

Urosaurus microscutatus [AMNH R-141087]

00100000111200000000001000?00001010000001000
00110001011021000?0?000001101?00200000000000
001???01000000011000100010100200000000000000
0000010100000010000000100011?00000000?030??0
00121?20?0?0???11010?000000?00100003000000000
000000012001?01?0100110100000100001?0011{01}
0002000011100100?1000100000001?0?0?1?100?00?0?
?0?000?1???0?????????????????????????????????
?0000?00

[Scincomorpha—one species]

Hymenosaurus clarki [IGM 3/53]

1000?1?000020?0000000?30?0?000?000?10?020?00
000000110010000?0?1?0?111???0?00002101011000
2001?001???10011?00101?011100000?0000300?0??1
?0020?010?010?0???11?0???0000?0???010000?100
0000?0?????????101?1000000000?0???00?0?????????
???
???
????????????00???0

[Mosasauridae—four species]

Dallasaurus turneri [Bell and Polcyn, 2005]

????????????0?????????????????????????????????
???10????2???1????????????????????????????????
??1???
????????00???????1????????????????0202?11000??
?00???120002?1???110110?0211????????????????
???0000?0???1??100????????????????????????????
??0? ??

Judeasaurus tchernovi [Haber and Polcyn, 2005]

2?0?1?0001???00???????0???10?0????????????0?010?0?
011?10?01?0?0????0011?0?0?0?0?011?002102?00??

????1??
 ?1???10????????????100???2???????1?1?1????????
 0000000000???000????????????????????????????
 ???
 ???

Russellosaurus coheni [Polcyn and Bell, 2005]

21???1?00011?2000?????0?0?110???0100?0???00001
 001?1102000?0???0001101110101000000000110001
 1010001????1???00?001?011?????0?0000000?0200?0
 010?0110001100???11?010?00101203100110001?2??1
 0?1101101?011000?1001011202001000000000?????
 ???
 ???
 ??????????????????0?00?0?0

Yaguarasaurus columbianus [Páramo, 1994;
 Páramo-Fonseca, 2000]

311???1?0001212000?????000?1101010000???0???000
 1000101101010???0?111011100000000000011000
 11011001?01?011100000101?1211110?0000000?0?2
 00?00000?10000?100???11?011?1?1???????10?????
 0????????????????????1202001000?00000???1???2???
 ??????01????????????????????????????????????
 ???
 ??????????????0?0?0?0

[Glyptosaurinae—two species]

Paraplacosauriops quercyi [Augé and Sullivan, 2006]

?????11????????????????00?1????????????????
 ???
 ???
 ?01?????00000211?0?????????????????????060000001
 01?001????????????????????????????????????
 ?????????????????????2?????1???002????????
 ?????????????????????????????????????0??0

Placosaurus rugosus [Sullivan and Augé, 2006]

?????1?11????????10????????0000?0????????
 101000100?01?00101????????????????????
 ???
 ???
 ???
 ?????????????????1?????1???22????????
 ?????????????????????????????????0

[new taxon]

Ovoo gurvai [IGM 3_767]

211???1?000110100100001300111100010001?101000
 00????110?002000110?01?0010????????????10001
 10?1???10?1101110111020101??0?101????????
 ???
 ?????????1202001100101000????????????
 ?????????????????????????????????????
 ?????????????????????????????????????
 ???02?0

APPENDIX 2

NEW CHARACTER DESCRIPTIONS

Here we offer descriptions of the nine new characters used in this analysis. These are numbered for placement at the end of the matrix in Conrad (in press).

365. Midline contact of the otooccipitals: (0) absent; (1) present.
366. Splenial, dorsal contribution to Meckel's canal: (0) absent; (1) present.
367. Crista circumfenestralis: (0) absent; (1) present; (2) present with posterior closure.
368. Forked posterior margin of the angular: (0) absent, (1) present.
369. Anterodorsal epicoracoid flange of the scapula (not an accessory scapular bar, but a crest): (0) absent; (1) present.
370. Margins of the lacrimal foramen: (0) shared between lacrimal and prefrontal; (1) within the lacrimal; (2) between the prefrontal and maxilla.
371. Anterolateral frontal flanges (if possessing a W-shaped nasofrontal suture): (0) short, not extending anteriorly as far as the midline part of the frontal; (1) subequal in anterior extension to the midline portion; (2) extending well anterior to the level of the midline portion.
372. Location of the fleshy, external nostril: (0) distally placed, near the anterior third of the snout; (1) placed in the middle 1/3 of the snout; (2) placed near the eye. Note that the character states for this character are somewhat subjectively defined, but the "bins" do describe observed morphology.
373. Prefrontal bones and postorbital arch arching toward each other: (0) absent; (1) present, approaching without contact; (2) contacting.

APPENDIX 3
DATA MATRIX

Character-state matrix for the new characters to be added to that of Conrad (in press). Note that these codings may be cut from the (free) pdf available from <http://library.amnh.org> and added to the matrix of Conrad (in press) available from the same website. Note thatAMNHgekkonomorph refers to AMNH FR21444 (Conrad and Norell, 2006), PseudosaurillusSP refers follows usage of Estes (1983), AMNHiguana refers to IGM 3/858 (Conrad and Norell, 2007), FMNHiguana refers to FMNH FR 2379 (Conrad et al., in press), and AnoleAMBER refers to the published anoles preserved in amber (Lazell, 1965; Rieppel, 1980b; de Queiroz et al., 1998).

| | | | |
|-------------------------|--------------|-----------------------|-----------|
| RHYNCHOCEPHALIA | 0?000-{01}00 | Eurheloderma | ???????0 |
| Huehuecuetzpalli | ?????0?0 | Heloderma_suspectum | 000???-00 |
| AMNHgekkonomorph | 0????1?0 | Heloderma_horridum | 000???-00 |
| Gobekko | 0?????0?0 | Heloderma_texana | 0?0????0 |
| DIPLODACTYLINAE | 0?????-00 | Lowesaurus | ???????? |
| Tepexisaurus | 0????0?0 | Gobiderma | 000????? |
| Eolacerta | 0???????0 | Paraderma | ???????0 |
| GYMNOPHTHALMIDAE | 010????00 | Primaderma | ???????? |
| Prototeius | ???????? | Ophisaurus_ventralis | 00?????00 |
| Chamops | ???????? | Ophisaurus_attenuatus | 00?????00 |
| TUPINAMBINAE | 000????00 | Dopasia | 00?????00 |
| TEIINAE | 0?????00 | Pseudopus | 000????00 |
| PseudosaurSP | ???????? | Parophisaurus | 0???????0 |
| Pseudosaurillus | ???????? | Anniella | 000????00 |
| LACERTIDAE | 0?????00 | Anguis | 000????00 |
| Ornatocephalus | ???????? | Apodosauriscus | ???????? |
| CORDYLOIDEA | 000????00 | Celestus | 00?????00 |
| Sakurasaurus | ???????? | Diploglossus | 00?????00 |
| Parmeosaurus | 0???????0 | Ophiodes | 00?????00 |
| Xenosaurus | 000???000 | Paragerhonotus | ???????0 |
| Lancensis | ???????? | Gerrhonotus | 000????00 |
| Carusia | 000???1?0 | Barisia | 000????00 |
| Exostinus | ???????? | Elgaria_multicarinata | 000000100 |
| Restes | ???????? | Abronia_deppii | 000????00 |
| Colpodontosaurus | ???????? | Xestops | ???????? |
| Eosaniwa | 0???????0 | Proglyptosaurus | ???????00 |
| Parviderma | ???????? | Glyptosaurus | 00?????00 |
| Bahndwivici | ???????? | Paraglyptosaurus | ???????? |
| Shinisaurus | 000????00 | Helodermoides | 00?????00 |
| Dalinghosaurus | ?0000???0 | Placosaurus_rugosus | ???????? |
| feisti | ???????? | Melanosaurus | 0???????0 |
| Necrosaurus_cayluxi | ???????? | Proxestops | ???????? |
| Necrosaurus_eucarinatus | ???????? | Odaxosaurus | ???????? |
| Proplatynotia | 00???1?0 | Paraplacosauriops | ???????0 |
| Paravaranus | 0????2?0 | Peltosaurus | 0?00????0 |
| Parviraptor_cf_estesi | ???????? | Arpadosaurus | ???????0 |
| Parviraptor_estesi | ???????? | Ophisauriscus | 0???????0 |
| Saniwides | 00????0?0 | Bainguis | 0???????0 |
| Telmasaurus | 0???????0 | Parasaniwa | ???????0 |
| Lanthanotus | 000???-00 | Dorsetisaurus | 000?????0 |
| Ovoo | ????02?0 | otherMACROSTOMATA | 102????00 |
| Aiolosaurus | ?0?????0 | Xenopeltis | 1?1????00 |
| Palaeosaniwa | ???????? | ANILIOIDEA | 101????00 |
| Estesia | 0?0????0 | Dinilysia | 1?2????0 |

| | | | |
|---------------------------------|-------------|---------------------------|-------------|
| Haasiophis | 10?????0 | Ctenomastax | 00?????0 |
| Pachyrhachis | 1???????0 | Temujinia | 00?????0 |
| Eupodophis | ????????? | Rhampholeon | 0-0?????00 |
| Pachyophis | ????????? | Brookesia | 0-0?????00 |
| Wonambi | 1?2?????0 | Physignathus | 0-0?????00 |
| Bavarisaurus | ????????? | Pogona | 000010000 |
| Ardeosaurus | ????????? | Hydrosaurus | 000000200 |
| Eichstaettisaurus | ????????? | Agama | 0-000??00 |
| Yabeinosaurus | ????????? | Uromastyx | 0-0?????00 |
| Scandensia | ????????? | Phrynosomimus | ????????? |
| Aphanizocnemus | ????????? | Priscagama | ????????? |
| Dolichosaurus | ????????? | Mimeosaurus | 0????????? |
| Coniasaurus | ?0???????0 | AMNHiguana | ????????? |
| Adriosaurus | ????????? | FMNHiguana | ????????? |
| Pontosaurus | ????????? | ANISOLEPINAЕ | 000?????00 |
| Aigialosaurus | ????????? | LEIOSAURINAЕ | 000?1??00 |
| Opetiosaurus | ?0???????0 | Polychrus_marmoratus | 00000??00 |
| Judeasaurus | ????????? | Polychrus_femoralis | 00000??00 |
| Tethysaurus | ????????? | Polychrus_gutturatus | 0000??000 |
| Russellosaurus | 0?00??-?0 | AnoleAMBER | ????????? |
| Yaguarasaurus | 0?0??-?0 | Anolis_heterodermis | 0-00?????00 |
| Carsosaurus | ????????? | Isodontosaurus | ?0?0????? |
| Pluridens | ????????? | Anolis_occidentalis | 00001??00 |
| Goronyosaurus | 0?0?????0 | Anolis_vermiculatus | 000-0??00 |
| Halisaurus_arambourgi | ???0????? | Leiocephalus | 000?????00 |
| Halisaurus_platyspondylus | 0????????? | Stenocercus | 000?????00 |
| Halisaurus_sternbergii | ????????? | Liolaemus | 00000??00 |
| Plotosaurus | 0?0?????0 | Hoplocercus | 00001??00 |
| Globidens | ????????? | Morunasaurus | 0001??000 |
| Mosasaurus_lemonnieri | 0????????? | Enyalioides | 000?????00 |
| Mosasaurus | ?0???????0 | Oplurus_quadrumcinctatusA | 0-0?????00 |
| Rikisaurus | ????????? | Oplurus_cyclotus | 000?????00 |
| Clidastes | 0?0?????0 | Oplurus_quadrumcinctatusB | 0-0?????00 |
| Platecarpus | 0?0?????0 | Chalarodon | ?-0?????00 |
| Prognathodon_overtoni | 0????????? | Polrussia | 00????????? |
| Prognathodon_solwayi | 0?0?????0 | Igua | ?00?????0 |
| Plioplatecarpus | 0?0?????0 | Myrmecodaptria | ???0????? |
| Ectenosaurus | ????????? | Eidolosaurus | ????????? |
| Tylosaurus | 0?0?????0 | SCELOTINAЕ | 0?0?????00 |
| Hainosaurus | 0????????? | ACONTINAЕ | 0?0?????00 |
| Lakumasaurus | ????????? | Hymenosaurus | ?000????? |
| Palaeoxantusia | 00????????? | SCINCINAЕ | 010?????00 |
| Xantusia | 000?????00 | FEYLINAЕ | 0?0?????00 |
| Cricosaura | 000?????00 | Meyasaurus | ????????? |
| Lepidophyma | 000?????00 | Slavoia | ?0????????? |
| Polyglyphanodon | ?0?0????? | Tchingisaurus | ????????? |
| Erdenetesaurus | 00?0????? | Dibamus | 0-0?????00 |
| Adamisaurus | ????????? | Anelytropsis | 0-0?????00 |
| Cherminisaurus | ?0????????? | Eoxanta | 0????????? |
| Gobinatus | 00?1????? | Hoyalacerta | ????????? |
| Darchansaurus | ?0?0????? | Globaura | 000?????00 |
| Macrocephalosaurus_chulsanensis | 0000????? | Gonatodes | 0-0-0??00 |
| Sineoamphisbaena | ?0?0????? | Gekko | 0-0-0??00 |
| Blanus | 0-0?????00 | Pachydactylus | 0-000??00 |
| AMPHISBAENIDAE | 0-0?????00 | Teratoscincus | 0-000??00 |
| Cherminotus | 0?????1?0 | Aeluroscalabotes | 00000??00 |
| Zapsosaurus | 0????????? | Hemitheconyx | 0-000??00 |
| Anchaurosaurus | 0????????? | Coleonyx | 00000??00 |

| | | | |
|------------------------|-------------|-------------------------|--------------|
| Paramacellodus | ?0?0???? | Leptotyphlops | 101 --- ?00 |
| Becklesius | ?0?????? | Pygopus | 0000 --- ?00 |
| Varanus_olivaceus | 0?00?0210 | Aprasia | 0000 --- ?00 |
| Varanus_eremius | 0000?0210 | Delma | 0000 --- ?00 |
| Varanus_tristis | 0000?0210 | Pletholax | 0000 --- ?00 |
| Varanus_semiremex | 0000?0210 | Dallasaurus | ???????? |
| Varanus_kordensis | 0?00?0210 | Dipsosaurus | 0-00?0100 |
| Varanus_prasinus | 000010210 | Brachylophus | 0-0000100 |
| Varanus_salvadorii | 0000?0200 | Armandisaurus | ????????0 |
| Varanus_priscus | ???????? | Crotaphytus_bicinctores | 000000200 |
| Varanus_komodoensis | 000??0200 | Gambelia | 000000000 |
| Varanus_varius | 0????100 | Crotaphytus_collaris | 000000100 |
| Varanus_gouldii | 000000210 | Basiliscus | 0-0010001 |
| Varanus_acanthurus | 000000210 | Aciprion | ????????0 |
| Varanus_dumerilii | 000000-10 | Corytophanes | 0-0010-02 |
| Varanus_bengalensis | 000000010 | Microlophus | 0-0????00 |
| Varanus_rusingensis | ???????? | Plica | 0-0000200 |
| Varanus_flavescens | 0000?0210 | Callisaurus | 0-0000000 |
| Varanus_griseus | 0?0?0220 | Petrosaurus | 0-0100200 |
| Varanus_niloticus | 000010220 | Phrynosoma | 000-00-00 |
| Varanus_exanthematicus | 000010220 | Sceloporus | 000000200 |
| Varanus_indicus | 000010210 | Urosaurus | 0?0000-00 |
| Saniwa_ensidens | ?????1?0 | Bipes_biporus | 0-0 --- 200 |
| Typhlops | 101 --- ?00 | RHINEURIDAE | 000????00 |
| Liotyphlops | 101 --- ?00 | TROGONOPHIDAE | 0-0????00 |

Complete lists of all issues of the *Novitates* and the *Bulletin* are available at World Wide Web site <http://library.amnh.org/pubs>. Inquire about ordering printed copies via e-mail from scipubs@amnh.org or via standard mail from: American Museum of Natural History, Library—Scientific Publications, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009.